# NOTES ON THE LIFE HISTORY, PARASITES AND INQUILINE ASSOCIATES OF ANTHOPHORA ABRUPTA SAY, WITH SOME COMPARISONS WITH THE HABITS OF CERTAIN OTHER ANTHOPHORINAE (HYMENOPTERA)

BY THEODORE II. FRISON

Urbana, Illinois

Not many years have elapsed since Ashmead (1894), in his retiring address as President of the Cambridge Entomological Club, said in regard to the genus Anthophora that "Almost nothing is known of the nesting habits of our species." When this quotation was written our literature contained only a few short contributions to the life history of the American species of Anthophora. The first account is that given by Walsh (1868) and deals with certain phases of the biology of Anthophora sponsa Smith, as he observed them in Illinois. The Anthophora sponsa of Smith is now considered by the authorities on the subject as identical with Anthophora abrupta Say, the latter name having priority. Riley (1877) also published a few observations on the habits of Anthophora sponsa in connection with the description of a new genus and species of Meloidae found infesting the cells of this mining bee. In addition to these accounts, Say (1837) added to his specific description of Anthophora taurea a few observations on the habits of this species. This latter bee, however, is no longer regarded as belonging to the genus Anthophora. It was first removed by Patton (1874) when he erected the genus Entechnia, making taurea of Sav the type. Since then this generic assignment has been adhered to by the authorities on the group. In the most recent list of the North American Anthophoridae, by Lutz and Cockerell (1920), taurea is still retained in the genus Entechnia, but the authors state "It seems quite probable that the name Entechnia must give way to Melitoma." As the two genera involved are closely related, in fact belong to the same subfamily, the original observations of Say are doubly interesting from a comparative standpoint. Since the time of Ashmead's address some additional information has been obtained concerning the habits of a few species of the Anthophorinae and certain other insects that live in their cells and burrows. Reference is given to all such publications of interest from the standpoint of this article as they are mentioned in the text of this paper.

### A. NEST SITUATIONS

My attention was first called to a colony of Anthophora abrupta Say, when collecting insects near Oakwood, Illinois in the Spring Oakwood is a small town about twenty miles east of Urbana, Illinois. Within a radius of two or three miles of Oakwood are many small areas, ecologically quite different, which offer ideal collecting grounds for this section of the state. One day while collecting Hymenoptera on flowers near the margin of a small rocky stream in this territory, I chanced upon several bees of this species eagerly lapping up moisture held by the fine sand bordering a tiny rivulet flowing into the main channel. As I watched I saw these bees hurriedly leave and others take their places, the whole performance being repeated again and again. As their going and coming seemed to be over a definite course I decided to follow them to their rendezvous if it were possible. In so doing I soon realized that the bees in their flight were following the line of least resistance, in this instance a passage-way, broken through the underbrush lining the river bank, and used by fishermen and other wanderers as myself. Scarcely two hundred feet from where I saw the bees zealously lapping up water I came upon a small clay bank which appeared literally alive with them. Figure 1 is a photograph of this bank, taken on July 11, 1919.

For various reasons I was unable to make further observations on the habits of this species in 1917 and 1918, but an opportunity was again presented in 1919 and 1920. One of the outstanding features of the habits of the adult Anthophora abrupta is its preference for the old colony site, at least such was the case with the members of this colony. This is evident when one considers that nearly all my observations relating to this species are centered about this one colony, first found in the late Spring of 1917, tenanted in 1919 and 1920, and with

every indication that the same state of affairs existed in 1918. The clay bank in which the bees made their homes was about three feet high, two to three feet wide and twelve feet long. It was situated but a short distance from the river beneath a steel bridge connecting with the opposite bank and beside one of the concrete foundations supporting the structure. Here the bank was in a semi-protected situation, but still at times exposed to the glare of the sun and rain blown about by the wind. To all appearances, the clay bank was simply a pile of clay removed by workmen when engaged in excavating for the concrete foundation pillars of the bridge. The clay was the same as that found anywhere along the river and any number of situations possessing about the same qualifications might have been selected by these mining bees.

Besides the colony just mentioned I found another one of the same species in the same year. This also was at Oakwood, Illinois, but on the opposite side of the river and about an eighth of a mile from the first colony. It is interesting to note that again I located the colony by following the flight of the bees returning to their homes after collecting water at the river bank for their mining operations. When I first came upon the bees going and coming from the moist sand near the river's edge, I knew by reason of previous experience the significance of this and immediately looked about for the site of the colony. This happened to be the precipitous clay wall of the river bank, not far from where the bees were obtaining their water supply. The colony was situated just below a large tree growing on the very brink of the almost perpendicular clay wall. Here, in the clay more compactly held together by the major root system of the tree, the bees had made their burrows. The colony was only about one-fifth the size of the one under the bridge and so hard of access that I made no further study of it.

When speaking of the situations selected by Anthophora abrupta for their mining operations it is interesting to note what other authors have to say concerning this species and certain other Anthophorinae. Walsh found this species making burrows in the mortar between joints in brick work and also in "the face of a precipitous clay bank." Riley says this same

TRANS. AM. ENT. SOC., XLVIII.

species "builds mostly in steeply inclined or perpendicular clay banks." Evidently, judging from my observations and those of Walsh and Riley, Anthophora abrupta has a preference for a perpendicular or steeply inclined surface. Under natural conditions a compact clay bank is usually selected, for such a soil type seems better adapted to the peculiar mining activities of this bee and does not weather away so rapidly. A similar preference is exhibited by Anthophora stanfordiana Cockerell, a western species. Kellogg (1905) found a colony of this latter species near Stanford University, "in a roadside cutting exposing a clayey bank." Nininger (1920) reports finding two colonies of this same species occupying on one occasion, "the sunny slope of a moist clay bank in the foot hills of the San Gabriel Mountains of southern California", and another time, "a steep bank, facing south at the shore of the bay", on Angel Island.

Similar and different nest situations are chosen by allied bee genera. Say writes that Entechnia taurea "digs a cylindrical hole in a compact clay or adhesive earth on the side of a bank, or in earth retained amongst the roots of an overturned tree." Upon one occasion I found a colony of this same species located in a perpendicular clay bank beneath a railroad bridge crossing a stream at White Heath, Illinois. Clisodon terminalis Cresson, according to the late F. W. L. Sladen (1919), nests in wood and thereby differs biologically from the genera Anthophora, Entechnia and Emphor. Nichols (1913) has given us an account of the situation selected by Emphor fuscojubatus Cockerell. species made numerous nest openings, "by the side of a road, for a distance of about one-eighth of a mile, in soil consisting of a mixture of clay, sand and pebbles." Grossbeck (1911) says that Emphor bombiformis [ = fuscojubatus] "seems to prefer hard, shaly soil in which to nest though small colonies occur in sandier soil."

## B. Size of Colonies and Gregarious Habits

A glance at figure 1 will show the portion of the bank occupied by the bee burrows and figure 2 shows how close the burrows are to one another. In order to get some idea as to how many bees belonged to this colony and to examine the contents of the cells, I dug from a fairly representative section of the bank

a piece containing about eight cubic inches of the hard, dry elay. This was on May 31, 1919. In a portion of this elay lump, containing two and one-half cubic inches of soil. I found eleven cells containing pupae of this bee. If the entire bank supported such a proportion it would have a total of one hundred and four thousand, two hundred and seventy-four cells. Such was not the case, however, for the burrows were most abundant on the upper part and on the most precipitous side. In 1921 the bees were harder pushed for desirable locations, for many made their burrows all over one end and some even took possession of the flat top surface. In many places the burrows and cells went back into the clay bank ten or twelve inches. A conservative estimate would indicate that in summer this Anthophora bank harbored about five thousand cells. A marked gregariousness is therefore exhibited by these so-called solitary bees. The same tendency towards a social type of existence characterizes the habits of Anthophora stanfordiana, Kellogg mentions a "great colony" of these bees and Nininger says that one colony of this same species occupied an area "extending over several square rods" and that it contained several thousand bees, while a second community was but "a small aggregation." Judging by Say's account of the habits of Entechnia taurea, as he observed them in Indiana, and by what I have noted in Illinois, these bees also like to nest close together. The colony of this latter species that I found at White Heath, Illinois, was composed of not over three hundred cells. Nichols says that Emphor fuscojubatus made numerous nest openings in the soil by the side of the road for a distance of about "one eighth of a mile." There is nothing in her account to indicate that these bees ever formed such concentrated colonies. Grossbeck, however, found several colonies of this same species of bee scattered short distances from one another, the largest having in the neighborhood of seventy bees, and the smallest eight to twelve bees each. The fact that Clisodon terminalis burrows in wood much in the manner of Xylocopa suggests that very large colonies are a rarity if they ever occur. It was once my fortune to rear adults of Melissodes bimaculata Lepeletier from cocoons found after they had been exposed by plowing. Apparently this species of Eucerine bee has habits comparable

TRANS. AM. ENT. SOC., XLVIII.

with those of many of our common solitary bees. Ashmead has seen the same species of bee entering its burrow beneath a stone in an open field.

#### C. HIBERNATION

Like many other Hymenoptera this bee hibernates as a larva within its cell. I have never examined an Anthophora bank during the winter months, but have other evidence in support of this statement. A visit to Oakwood on September 20, 1919. revealed the fact that the cells then contained full grown larvae. At this time I again brought back to the laboratory a lump of clay containing Anthophora cells. I divided this in halves. placing one portion in an old deserted bee-hive outdoors, thus subjecting the cell inmates to almost natural winter conditions. The other portion I kept in the laboratory under temperature conditions averaging about seventy degrees Fahrenheit. In March, 1920, I examined these two separate lots of Anthophora cells. On this date the inmates of the cells kept outdoors under approximately natural winter conditions were still in the larval stage. Those kept in the laboratory were still in the larval stage in February, but the influence of warmer conditions caused the larvae to begin to pupate in March. Thus we see that this bee normally hibernates in the larval stage protected by its earthen cell.

#### D. Cell Formation

The adult bees use some liquid substance when first fashioning the cell, and it is probable that the larvae when they attain their full growth also contribute something to give the cell its characteristic durability. When a clod of clay containing these cells is broken apart, under ordinary conditions of stress the cells never collapse but hold their shape and may be readily sorted out from the débris. This again is proof that the bees and perhaps the larvae use a cementing substance. When a cell is broken open its inner lining has a smooth glazed appearance. This is due to the substance used in forming the protective cell and causing it to retain its characteristic shape. A complete cell is usually slightly recurved at its anterior end, which is an indication that the cells radiate off from the main stem-burrow which leads to the entrance of the nest. The

interior measurements of the cells average sixteen millimeters long by nine millimeters wide. Cells freed from all soil not actually entering into the formation of the same average twenty-five millimeters long and have a diameter of ten millimeters at the anterior end and twelve millimeters at the posterior extremity. Several times I have opened the over-wintering cells, removed the larvae within and then filled the cells full of water. On such occasions it was evident that the substance which held the cells together and gave them a glazed appearance on the inside, also served to make the cells impervious to water. Such a protection against soil moisture would seem to be a necessity in the case of bees like these which do not spin a silken cocoon within their surrounding cell.

I am sure that the adult bee when making her brood cells waterproofs them with some secretion. If she did not do so the semi-fluid mass of pollen and nectar on which she lays her eggs would be partially absorbed by the cells. Nininger speaking of Anthophora stanfordiana says that this bee in making her cells used "a thin layer of waterproofing which seemed to be a salivary secretion." Whether the larvae of any or all instars further improve the cell resistance by secretions or exudates I do not know. The larvae do not spin cocoons as do those of Melissodes bimaculata and many other bees not far removed phylogenetically or morphologically. If the larvae of Anthophora abrupta do improve their cells by a salivary secretion, it is possible that the basic substance of the cementing fluid used by this species, may be of a chemical composition quite similar to that of the silk spun by the larvae of Melissodes bimaculata. Another bee, Emphor fuscojubatus, differs biologically from Anthophora abrupta because of its cocoon spinning propensities, thus pointing to its closer biological relationship with Melissodes bimaculata.

#### E. PUPAL STAGE

The pupal stage of development is entered into under natural conditions about the middle of May, or at least such was the case in 1919 and 1920. This is evidenced by the fact that on May 8, 1920, when I visited the bee-bank at Oakwood the cells contained larvae. A similar visit and examination on May 31,

TRANS. AM. ENT. SOC., XLVIII.

1919, showed that the cells contained pupae. The period of pupal formation undoubtedly varies somewhat from year to year in direct correlation with climatal conditions. Under laboratory conditions the larval stage may be shortened and pupae formed about the first of March. On March 13, 1920, I brought into the laboratory some cells containing larvae which since the time of collection had been kept out of doors under approximately natural conditions. One of these cells contained a pupa on March 29. Other larvae in cells placed on September 20, 1919, under warm laboratory conditions, began to pupate in the early part of March. Such a forced expediting of the transformations under the influence of prematurely warm conditions apparently has a weakening effect, for an adult male emerging on March 18 died soon after escaping from his cell. Cells brought into the laboratory in Spring produced, however, adults of normal vitality.

The pupal stage is of short duration. Freshly transformed pupae collected at Oakwood on May 31, 1919, began to produce bees on June 7 and continued to do so until June 14. As the pupal stage nears completion the pupa gradually becomes darker and darker until the adult emerges. The emerging adults dig their way from the pupal cells with the aid of their stout mandibles. The males appear in advance of the females. as shown by both laboratory and field observations. Of the bees reared indoors in 1919, two males emerged on June 7, four males on June 8 and twenty-six more of the same sex on June 9. On June 11, eleven females emerged and enough more males to bring the total for that sex up to one hundred and four individuals. Females continued to appear until June 14, a total of sixty-five altogether. Cases of proterandry similar to this one seem to be quite common among bees, as was pointed out by Robertson (1918). Not only do the males appear first but in the colony I studied they dominated numerically by a ratio of about two to one. Observations at Oakwood in 1919 and 1920 confirmed my laboratory observations. On July 3, 1919, I visited the Anthophora bank and found a veritable swarm of female bees hovering about the bank and entrances to the burrows. Apparently I was just a little too late to see the males holding forth before the bank. On June 26, 1920, at the same

spot I witnessed the reverse of this phenomenon, for I saw only one female bee among the large number of bees flying about the entrance burrows. By breaking open some of the cells I discovered that the females were just beginning to emerge from their cells, the males having preceded them. I never found out what finally happened to the males, but judge that after they had mated with the females they spent the remainder of their short existence loitering about on flowers as do many male bees.

# F. MINING OPERATIONS AND ATTENDANT ACTIVITIES

The scene presented on July 3, 1919, was an animated picture of industry, for the females were busily engaged in their nest building operations. A few females, either more industrious than the rest or favored by a slightly earlier date of emergence, seemed to have completed their residences. The vast majority, however, were still in the midst of the construction of their subterranean homes or were looking for a favorable site in which to start their burrowing. Everything seemed to be in confusion, yet rapid progress was being made everywhere. I was not surprised to find that in several instances bees returning to the bank entered the wrong holes. When this happened and the rightful owner was at home, the invasion was hurriedly repelled as evidenced by a pronounced buzzing and the hasty exit of the invader. On one occasion I saw the proprietor of a burrow drag her unwelcome guest out by one leg. Several times the rightful occupant of the burrow and the invading bee were in such a close embrace that both fell out and down the precipitous side of the bank together. Strangely enough I never saw these bees while thus quarrelling attempt to sting one another. Such quarrelling among solitary bees living close together has been previously noted by Grossbeck in the case of Emphor bombiformis (=fuscojubatus). The same species, according to the observations of Nichols, "on the contrary, so far as we could tell lived together, mutually harmonious, yet independent." Individual differences no doubt exist between members of the same species, but I am inclined to believe that local conditions and varying circumstances were responsible for the differences noted by these two last mentioned authors.

TRANS. AM. ENT. SOC., XLVIII.

#### G. Entrance Tubes

As already mentioned some of the burrows were evidently completed on July 3, 1919. One strange feature about the entrance to the burrows are the cylindrical tubes extending down and outward from the entrance holes. Walsh undoubtedly refers to these tubes when he writes that Anthophora abrupta builds an entrance to its burrows "of tempered clay. . . about two inches long and three quarters of an inch in diameter." Say, referring to the habits of the European Anthophora parietina Latreille, says that this species digs a hole in a clay bank and that the "entrance consists of a cylinder extending downwards from the mouth of the hole more than an inch in length and consisting of small pellets of earth compacted together, very rough on the exterior and smooth within." Certain other insects are known to construct cylinders at the entrance to their underground burrows. The cylinders about the orifice of each tunnel at Oakwood varied from a quarter of an inch to four inches in length. The inside diameter of the cylinders was about one-half inch. The difference in length is probably due to the fact that some of the burrows were started sooner than others, though it is possible that under certain environmental conditions erratic individuals may make them very short or even neglect them altogether. It is to be noted that in figure 2 many of the holes lack an entrance cylinder, but it is probable in this case that many if not all of these are simply old uninhabited burrows. As in the case of Anthophora parietina the tubes are very smooth on the inside, rough on the outside and made of small pellets of clay removed from the inside of the burrow. One peculiarity of the tubes or cylinders is an open fissure on the uppermost portion, more noticeable in some examples than in others. Similar "bent-over chimneys of clay" were observed by Nininger, and also by Kellogg, over the entrances to the burrows of Anthophora stanfordiana. Entechnia taurea likewise makes such an entrance chimney over the burrows according to Say, who says "many of the tubes . . . . , have a fissure above, throughout the whole length." Riley reports finding these odd-looking chimneys extending from the entrance of the burrows of Anthophora abrupta, and has theorized concerning their purpose. This writer has suggested that these tubes make it difficult for the clumsy parasitic Meloid beetles to climb about the cells, and Kellogg says they prevent the "flooding of the open burrows by water." Walsh says the tubes serve to keep out parasites. If the tubes served in any way as a protection to the real entrance to the burrows of Anthophora abrupta, why is there this break in their continuity, especially upon the upper portion? Water could certainly gain entrance here and the rift is large enough to enable several of the smaller hymenopterous parasites to enter the tube. Furthermore, as the chimneys are open at the outer end I fail to see in them any effective barrier to the inroads of parasites. Emphor fuscojubatus, according to Grossbeck, builds little turrets one-half inch high around the entrance to the burrows and then drops the remainder of the pellets over the rim.

Watching the bees at their labors, I soon saw that the tube was formed by pellets of clay brought out from the burrows by the bees when engaged in their mining operations. After being in the burrows a short time the bees back out and carry with them, under the body, a small amount of wet clay. This explains why the bees were lapping up moisture when I first came across and followed them to their burrows in 1917. The bees go to a place where water is to be had and when they have lapped up all they can hold return to their burrows. Then they use the water to soften the hard clay in which they dig their burrows. If such is not the case how are we to explain the fact that the bees remove wet clay from burrows made in a hard dry clay bank? An interesting manner of obtaining water to use in their mining operations has been observed in the case of Emphor fuscojubatus. Grossbeck reports seeing adults of this species on the surface of roadside puddles, but was not sure they actually lapped up any of the water. Knab (1911) has observed Emphor bombiform is alighting on the surface of water and actually saw them lapping up the water. Nichols records the same curious habit for Emphor fuscojubatus, saving, "numerous bees were discovered floating on the surface [of a small pond with legs outstretched, presumably sucking up into their crops a supply of water for use in making the nest."

Instead of simply dropping the clay from the entrance of the burrows these bees instinctively make with it a cylindrical tube

TRANS. AM. ENT. SOC., XLVIII.

attached to the entrance of the burrow. When a bee reaches the end of the burrow or tube and has in its custody a wet pellet of clay it presses the pellet against the outer edge of the tube with the ventral surface of the abdomen and the posterior legs. The head and mandibles also take part in the final shaping of the pellet on the end of the tube. As this operation is performed in summer, the clay quickly dries and becomes an integral part of the tube. The exterior surface of the tube is never polished and hence remains rough. The interior surface, however, is smooth as a result of the polishing given it by the abdomen as the pellets are fastened on at the end. A similar instance of the abdomen "being used as a trowel" is recorded by Nichols for Emphor fuscojubatus. Grossbeck also has observed similar actions on the part of the same species. The fissure on the top of the tube appears to be due to the fact that Anthophora abrupta has an aversion to standing upside down while joining the pellets onto the tube. Not one of the bees I observed at this work ever assumed an absolutely upside down position, though all would work around on the edge nearly to the top. The definite course of each burrow was very difficult to trace. It seems that each female makes her own burrow and then digs lateral branches from the main stem which form the cells. I never managed to decide how many brood cells each female made and provisioned, but judge they are not numerous.

#### H. Anthophilous Habits

On July 3, 1919, some of the bees returning to the nest were loaded with pollen. Bees so engaged in pollen storing seemed to have less difficulty in finding their burrows than those still in the midst of their mining operations. This is probably to be explained on the basis of a longer acquaintance with, and occupation of, their burrows, coupled with associative memory. On July 11, 1919, all the bees flying to and from the bank appeared to be females and were busily engaged in storing their cells with pollen and nectar. Robertson (1891, 1894, and 1896), in Illinois, records males and females as visitors to Asclepias purpurescens, Hydrophyllum virginicum, Mertensia virginica, Convolvulus sepium, Pentstemon pubescens, Pentstemon laevigatus, Rosa humilis, Rosa setigera and Gillenia stipulacea. Banks

(1911) reports this species from *Ceanothus*. No doubt this list of plants visited by the bees of this species could be considerably increased and thus we are dealing with a polytropic bee.

## I, NIDIFICATION AND FEEDING HABITS OF THE LARVAE

The females of Anthophora abrupta in 1919 laid their first eggs some time between July 3 and July 11. On July 11, 1919, I found the eggs to be deposited on a very soft, almost watery paste of pollen. Judging by the anthophilous habits of the adults and certain habits of other bees I feel sure the fluid used to moisten the pollen was regurgitated nectar. In general the egg-laving habits are similar to those observed for Anthophora stanfordiana and Emphor fuscojubatus by Nininger, Grossbeck and Nichols. When the cells are broken open any of the watery paste of pollen that spills out and comes into contact with the soil surrounding the cell is quickly absorbed. This is further evidence that the cell of this bee is rendered impervious to soil water by some kind of treatment by the adult. Otherwise the earthen cell would absorb at least a portion of the regurgitated nectar, and the pollen mixed with it and stored in the cell as larval food would dry out. The eggs are pearly white and have the same general appearance as those of bumblebees (Frison, 1917). One egg that I measured was two and one-half millimeters long and somewhat less than one millimeter wide. A single egg is laid in each completed and stored cell, which is then tightly closed by the mother bee. It is worth noting that the pollen-nectar food mass has a very pungent and offensive odor. I have no data on the duration of the egg stage but presume it is a matter of three or four days. The emerging larvae attain their full development on the provisions placed in their cell by the female bee before the egg is laid and the cell closed. Kellogg states that in the case of Anthophora stanfordiana "the food is carried to the young in the open cell." Nininger, who studied the same species, says that this is not true and that the cells are tightly sealed after the eggs are laid. Therefore, Anthophora abrupta and stanfordiana hae very similar habits and probably no larvae of Anthophora are fed daily by the adult bees. According to both Grossbeek and Nichols the eggs of Emphor fuscojubatus are deposited upon a mass of pollen from Hibiscus moschatus, and the emerging larvae ac-

TRANS. AM. ENT. SOC., XLVIII.

cordingly develop without being fed by the parent bees. My last visit to Oakwood in 1919 was on September 20, and the cells then contained full grown larvae. No adults were observed at this time and as nidification was completed the bees had probably perished. The larvae at this time averaged about thirteen millimeters in length and five millimeters in their greatest diameter, and were of a lemon yellow color. It may be well to note at this place that, on September 20, almost all of the peculiar entrance tubes previously described had broken off and fallen to the foot of the bank.

## J. MISCELLANEOUS ADULT HABITS

No opportunity was presented for a close study of the habits of the adult bees. Besides those traits already noted in connection with phases of their home building a few others merit recording. The bees never emerged from their pupal cells until they were ready to take flight. In the laboratory when the bees emerged in screened cages they flew towards the nearest source of light and made desperate attempts to escape from their prison. In so doing they demonstrated the great muscular power correlated with their large mandibles by drawing together a great many of the individual parallel wires forming the mesh of the screened sides of their cage. With such strongly developed biting powers it is no wonder that these bees are so adept at mining in hard clay banks. During the night and early morning the bees were not active and rested on the sides and the top of the cage. When resting, the bees hung onto the wire by their mandibles assisted by one or more pairs of legs. This position was also assumed when the bees cleaned parts of their body and legs. The disposition of the female Anthophora abrupta is very inoffensive. One can stand within a foot of the entrance holes to the burrows in the bank without danger of being stung. Even when I removed the cells from the bank swarming with females no resistance was encountered in spite of the fact that the females are armed with a good-sized sting. Such would not be the case with many social Hymenoptera, as anyone who has removed a bumblebee or wasp nest can testify. While I was seated on the ground near the bank watching their

movements, the bees would frequently alight on my hands and lap up drops of perspiration. They would even settle on and explore my camera outfit as if in search of a possible supply of moisture. No doubt the female will sting when picked up and roughly treated, but having had experience along this line with other bees I did not wish to try the experiment. In captivity these bees fed readily on a solution of honey and water.

## K. Observations on Parasite and Inquiline Associates

Continued occupation of the same bank year after year by large numbers of the same species of bee would seem to offer favorable opportunities for inquilinous and parasitic species of insects to become abundant. Riley has described a coleopterous insect by the name of Hornia minutipennis as occurring in the cells of this species. Another Meloë found in the cells of Anthophora occidentalis Cresson, has been described as Hornia gigantea by Wellman (1911), and according to Cockerell (1905) Mr. S. A. Johnson has found Leonidia neomexicana Cockerell in the cells of Anthophora bomboides. Though I have examined hundreds of cells of Anthophora abrupta I have never chanced upon a specimen of Hornia, but have found several other parasitic and inquilinous insects in the cells and burrows of these bees.

On May 31, 1919, I observed many specimens of an anthomyild flying about the entrance holes. I caught fifteen of these flies and Mr. J. R. Malloch kindly identified them for me as Pegomyia affinis Stein. They were also found flying about the bank in the same manner on June 20, 1920, when the males were first beginning to emerge. Indoors in 1919, Pegomyia affinis began emerging on June 8 and continued appearing until June 14. As in the ease of Anthophora abrupta, the males of this fly appeared first, my initial record for the appearance of the female flies being June 11. Hibernation is accomplished in a puparium in the old cells and burrows of the bees. I have never found any evidence that would indicate that larvae of Pegomuia affinis were ever parasitic. It seems that, after mating; the adult flies lay their eggs in and about the bee burrows when the bees are storing their cells. The emerging larvae then feed upon any waste products available and are therefore scatophagous. It may be that the eggs are sometimes laid in

TRANS, AM. ENT. SOC., XLVIII.

the stored cells before they are closed, and the rapidly developing fly larvae cause the female bees to abandon them before they have finished with their provisioning. I have never found the puparia in a properly sealed cell, but several times have found partially opened cells which contained a large number of them. Usually ten or twelve puparia occurred near one another in the infested burrows. As adults of *Pegomyia affinis* were observed flying about the holes in the bank on September 20, it is probable this fly has more than one generation a year.

A true parasite of Anthophora abrupta is found in the bombyliid fly Spogostylum albofasciatum Macquart (det. J. R. Malloch). I first found the larva of this parasitic fly on May 31, 1919, in a bee cell. This larva transformed to a pupa on July 5 and emerged as an adult on July 26. On December 30, 1919, and April 9, 1920. I found two other larvae of this species in cells of Anthophora abrupta. Various other investigators have found Spogostulum albofasciatum to be a parasitic species. There is also a probability that the larva of this bombyliid, after having destroyed the bee egg or killed the larva, will feed on the pollen stored in the cell. I am certain, however, that no bees develop from cells that produce these flies, and therefore Anthophora must fall a victim to the fly larvae in either the egg or larval stages, sometime before the advent of fall and winter conditions. Malloch (1917) describes and figures the pupa of this species and gives a good general account of the inquilinous, predaceous and parasitic habits of this family.

Probably the worst fly parasite of this bee is a conopid. Unfortunately I have never been able to rear the adult. The puparium is quite similar to that of *Physocephala sagittaria* Say, a parasite of the bumblebees. I first found this parasite in dead and nearly dead bees which had fallen to the ground at the base of the bee bank at Oakwood on July 3, 1919. Dissection of these bees revealed the presence of the characteristic conopid larvae and in one specimen a recently formed puparium. In 1919 I tried to rear the adults of this fly but failed, due in some cases perhaps to poor conditions of humidity, but in five instances to the effectiveness of a secondary Hymenopterous parasite. Mr. A. B. Gahan very kindly named this secondary parasite for me as *Mestocharis williamsoni* Girault. It is interesting to note that this is the same species of *Mestocharis* that

emerges from the puparia of Physocephala sagittaria Say, a conopid attacking bumblebees, and strengthens my supposition as to the identity of the conopid enemy of Anthophora abrupta. The secondary parasites were first noticed emerging from a small hole in the cephalic end of the conopid puparia on July 15. An examination of eleven puparia on August 12 showed that five were victimized by this small parasite. Five of the remaining puparia were completely dried out on this date and one contained a dead adult which was not sufficiently developed to permit of identification as to genus or species. When I visited the bee bank at Oakwood on July 11, 1919, I picked up fortynine additional Anthophora adults killed or nearly dead by reason of conopid parasitism. Some of the bees so killed were laden with pollen. In some cases the bees found on the ground were still able to walk around a little, and now and then would move about by violent jerks. All such queer acting bees were found to contain conopid larvae. In such cases I found the body of the fly larva in the abdomen of the bee, with the long neck-like process bearing the mouth parts inserted through the point of articulation of the abdomen and the thorax. Evidently the bee lives for some time after the copopid larva starts to develop within the bee abdomen, but dies when the larva becomes almost or full grown, and severs some of the vital organs and nerve connections centered in the thorax and about the articulation of the thorax and abdomen. This probably explains the contortions and nervous movements of the dying parasitized bees. The conopid larva forms a puparium within the abdomen of its victim soon after the bee dies and probably in this stage hibernates during the cold season, anywhere the bee happens to fall to the ground. As the duration of the life of the host bee is comparatively short, the conopid must have but one generation a year.

As already mentioned I reared adults of Mestocharis williamsoni from the conopid puparia, which are thus secondary parasites and beneficial to the Anthophova. I first noted the adults issuing from a conopid puparium on July 15, 1919, and other emergences continued for a week or more. On August 12, 1919, I isolated five puparia which seemed to be parasitized by this

TRANS. AM. ENT. SOC., XLVIII.

little chalcid, the adults of which had not all emerged and were dead as a result of unfavorable rearing conditions. On October 27 I dissected these puparia. In order to escape, the chalcids first emerging make a tiny hole in one end of the punarium. This hole either by chance or instinct was made in all cases through one side at the anterior or head end of the hardened case. In one puparium without an emergence hole I counted out one hundred and fifty-two dead adult chalcids. In three others from which most of the adults had emerged, judging by the small emergence holes described above. I found from thirteen to twenty-two dead chalcids. In another somewhat broken puparium I found seventy-four adults. On the basis of these figures one conopid may produce a surprisingly large number of its enemies, which may possibly be produced through polyembryony. Another check on the rayages of the conopids appeared to be a bacterial disease. Of the forty-nine puparia picked up at the base of the bee bank on July 11, 1919, a majority of them at the time showed indications of such a disease.

Monodontomerus species (det. A. B. Gahan) is very likely a true parasite of Anthophora abrupta. The pupae of this large greenish chalcid were first found in the bee cells on May 31, 1919. As fifteen or more of these pupae, without surrounding cocoons, were found in a single cell containing no trace of any stages of the bee, I assume them to be parasites. The adults first began to emerge in the laboratory on June 11 and were very numerous in the cage on June 14. A careful examination of the surface of the bee bank at Oakwood on July 3, 1919, disclosed the fact that these parasitic hymenopterans were then abundant around the burrows and tubular entrance cylinders. I have no additional information relative to the habits of this species. It would seem that mating takes place in July and that the eggs are laid in or near the new bee cells. Another species of Hymenoptera was reared about June 1, 1919, from several brownish, rather loosely-spun silken cocoons found on May 31, 1921. Unfortunately the reared adults were lost and I do not know the species involved. These cocoons did not seem to be directly associated with closed cells and I can not state what the habits of this species are. In a cell opened on July 11, 1919, I found a fully developed bee pupa which I doubt was Anthophora abrunta. I tried to rear the adult but failed

and can only surmise it was that of some inquilinous or parasitic species of bee.

Mention should also be made of a fungous disease of the bee larvae. Some of the bee cells opened on May 31, 1919, contained shrivelled larvae covered with a whitish fungous growth. No doubt bacterial diseases also take their toll of the *Anthophora* bee population.

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#### Explanation of Plate V

Fig. 1.—Colony of Anthophora abrupta Say, at Oakwood, Illmois.

Fig. 2.—Close-up view of a portion of same bank occupied by *Anthophora abrupta*.